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EARLY STAGES OF *MIRACAVIRA BRILLIANS* (BARNES) AND REASSIGNMENT OF THE GENUS TO
THE AMPHIPYRINAE: PSAPHIDINI: FERALIINA (NOCTUIDAE)

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ABSTRACT. The egg, larva, pupa, and male genitalia of *Miracavira brillians* (Barnes) are described and illustrated, and observations are provided on the insect's life history and larval biology. *Miracavira brillians* is transferred from the Acronictinae to the Amphipyrinae: Psaphidini: Feraliina based on numerous larval, pupal, and adult characters. Both larval and adult features support our arguments that the Amphipyrinae and Psaphidinae are synonyms.

Additional key words: *Amphipyra*, *Apsaphida*, *Feralia*, *Paratrachaea*, *Viridemas*, *Ptelea*, countershading, non-resemblance

Miracavira brillians (Barnes, 1901), a handsome green moth with lichen-like patterning from the American Southwest, is a univoltine insect that flies during the summer-monsoon season. Barnes described *brillians* in the genus *Feralia* Grote from material collected in the Huachuca Mountains of southeastern Arizona. In 1937, Franclemont created the cuculliine genus *Miracavira* for moths that had been treated by earlier workers as members of the genus *Feralia* (or its synonym *Momaphana* Grote) that lacked (eye) lashes. He designated *Momaphana sylvia* Dyar as the type of the genus; although he did not specifically mention *brillians*, its membership was implied given its close similarity to *sylvia*. McDunnough (1938) continued to associate *Miracavira brillians* with *Feralia* Grote and placed it between *Psaphida* Walker and *Feralia* in his checklist of North American Macrolepidoptera. Franclemont and Todd (1983) moved *Miracavira* into the Apameini (Amphipyrinae), following the somewhat superficially similar genus *Phosphila* Hübner. Poole (1995) did not treat *Miracavira* in his monograph on the Psaphidinae. Recently Fibiger and Lafontaine (2005) moved the genus into the Acronictinae without explanation. Here we describe and figure the egg, larva, pupa, and male genitalia of *M. brillians*, provide notes on the insect's life history and larval biology, and transfer the genus into the Amphipyrinae: Psaphidini: Feraliina. In addition to *Miracavira*, the male genitalia of five additional psaphidine genera are figured and compared:

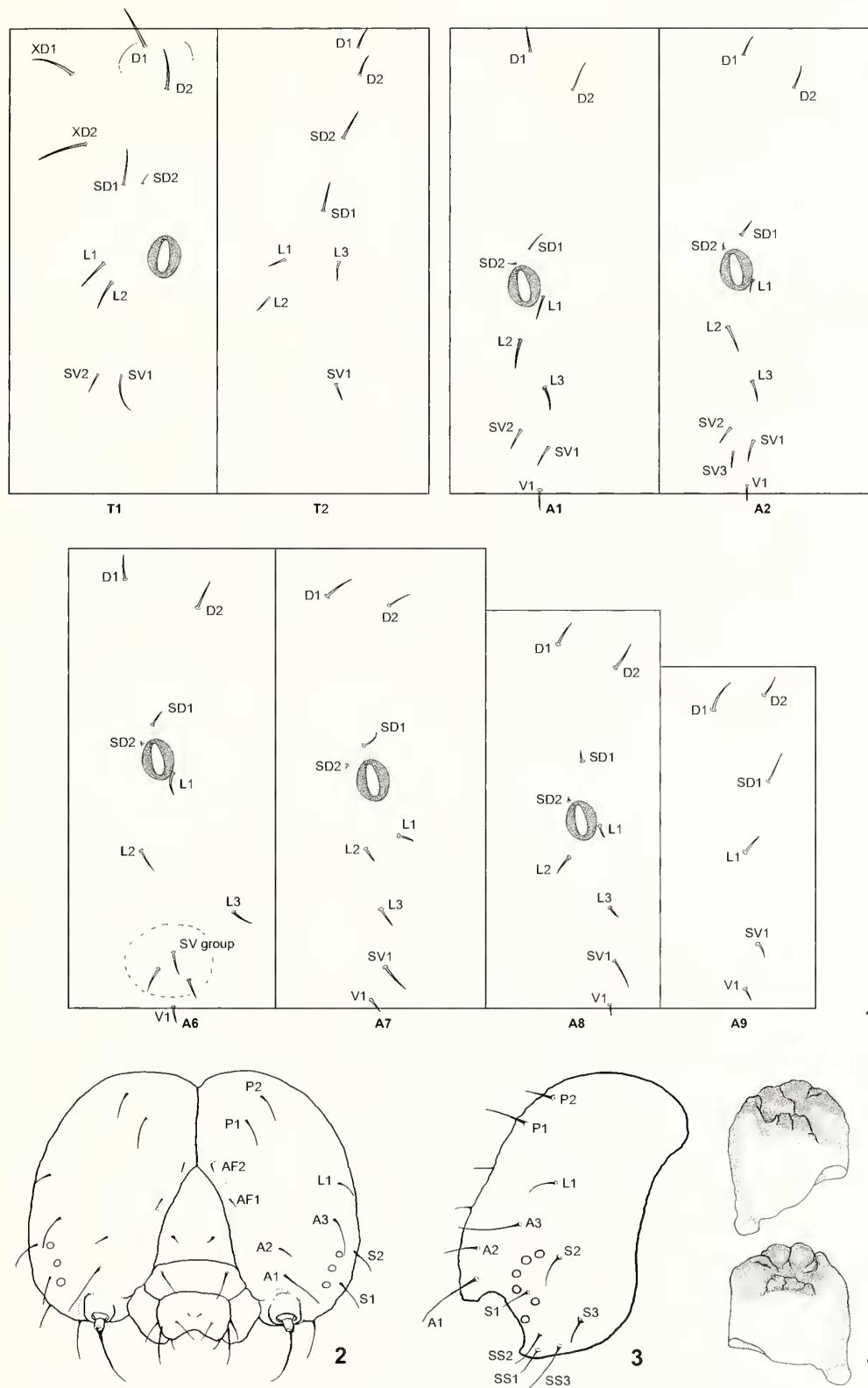
Apsaphida Franclemont, *Feralia* Grote, *Paratrachea* Hampson, *Psaphida* Walker, and *Viridemas* Smith. The paper concludes with an enumeration of structural and behavioral similarities of *Miracavira* and *Amphipyra* Ochs. and a brief discussion suggesting that the Amphipyrinae and Psaphidinae are synonyms (with the latter given tribal status).

MATERIALS AND METHODS

Eggs of *Miracavira brillians* were obtained from a female collected at UV light by NMcf on 16 August, 2006: AZ: Cochise Co., Hereford, Ash Canyon, 5,170 ft, oak-manzanita woodland. The female began laying eggs on the first night of confinement. Larvae were reared to maturity on *Ptelea trifoliata* in Hereford by NMcf and at the University of Connecticut by DLW and BC.

One larva was prepared for SEM study by running it through a series of ethanol baths (70%, 80%, 90%, 95%, 100%) before it was dehydrated with hexamethyldisilazane. The caterpillar was then coated with gold-palladium for three minutes in a Polaron E 5100 sputter coater. Images were obtained with a Zeiss DSM-982 Gemini FE SEM at 3 kV.

Six larval and one adult specimen and 57 film slide vouchers have been deposited at the University of Connecticut. Nomenclature, and in particular circumscription of the Amphipyrinae and Psaphidinae, follow the works of Kitching and Rawlins (1998) and Fibiger and Lafontaine (2005).

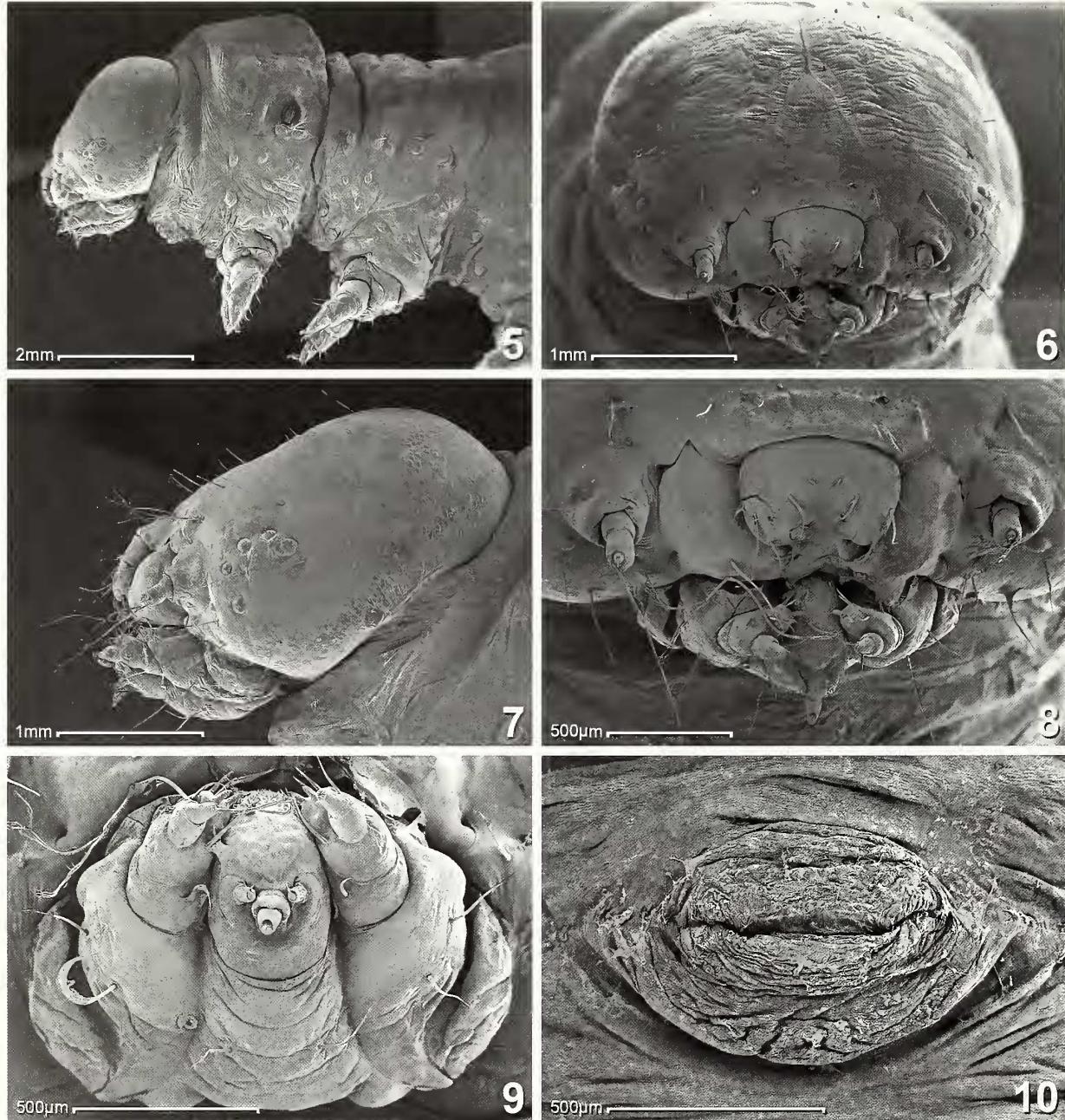
FIGS. 1-4. *Miracavira brillians* last instar. (1) Setal map. (2) Head, frontal. (3) Head, lateral. (4) Mandibles, mesal surfaces.

RESULTS AND DISCUSSION

Description of immature stages. Egg (Figs. 15, 16). Round, nearly as high as wide with 19–20 ribs; fewer than half of the ribs reach the micropylar area (n=12).

First-fourth instars (Figs. 17–20). Prolegs on A3 and A4 reduced, especially in the first instar. First instar (Fig. 17): Body translucent, shiny, with ground yellowish but coloration strongly influenced by (green) contents of gut; no white or cream markings. Larger pinacula black. No hump. Head pale orange-tan. Second instar (Fig. 18): Body wall translucent, emerald green with numerous creamy to white

spots; broken white middorsal stripe; thin continuous spiracular stripe; large; white spot below D1 and smaller creamy spot that includes D2 pinaculum. Larger pinacula black, thickened. Prothoracic ridge marked with white to creamy spots. Low hump over A8. Head subtly tinted with orange-tan. Third instar (Fig. 19): Emerald green, corrugated, with prominent creamy spotting; spiracular stripe much enlarged and fusing with lines that continue along leading edge of prothoracic and anal shields. Larger pinacula blackened. Spiracles without prominent black ring and halo of last two instars. Hump enlarged but without prominent middorsal protuberance. Head green with pale snowflake spotting and pale adfrontal edging along triangle.



Figs. 5–10. *Miracavira brillians* last instar. (5) Head to T2, lateral. (6) Head, frontal. (7) Head, lateral. (8) Mouthparts, frontal. (9) Maxillolabial complex. (10) Midsternal prothoracic gland.

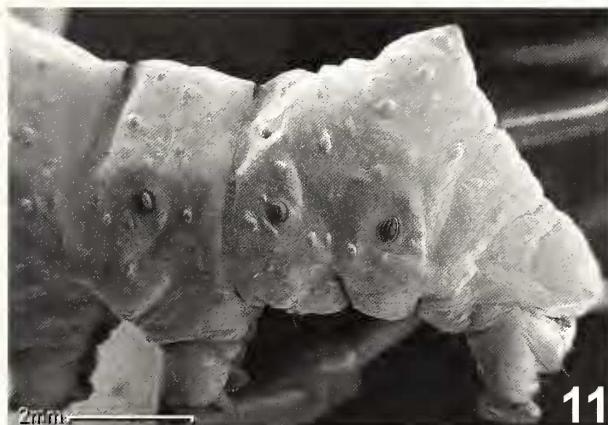
Fourth instar (Fig. 20): Green with conspicuous, wart-like yellow spotting, and well-developed middorsal and spiracular stripes; prothoracic and anal shields thickened, edged with pale yellow. Spiracles ringed with black and outer diffuse halo of waxy-blue white. A8 with middorsal yellow knob at apex of hump. Bluish white waxy bloom added over duration of stadium.

Living fifth instar (Figs. 21–22). Waxy blue-green, especially above with subtle pink, violet, or maroon hues and strongly humped eighth abdominal segment bearing bright yellow middorsal wart (Fig. 21); integument spotted with oval, cream to yellow, slightly elevated spots; these largest over dorsum and bases of prothoracic legs; spot diameters reduced below spiracular stripe; prominent chalky white middorsal stripe frequently broken over thoracic segments and A10; spiracular stripe pale and thin, with numerous embedded yellow spots, continuing forward around anterior and posterior rims of prothorax and anal plates, respectively; upper edge running just below lower reach of spiracles; often broken and incomplete anterior to A4. Pinacula inconspicuous. Prominent white and black spiracles. Anal prolegs short and held back, scarcely extending beyond anal plate. Anterior edge of prothorax yellowed, forming raised lip over head. Head as in Fig. 22.

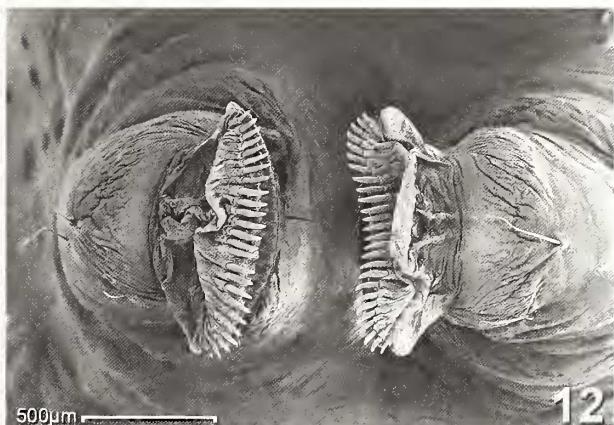
Preserved fifth instar (Figs. 1–14). Length: to 35 mm (n=4). Essentially unpigmented save for conspicuous enlarged and darkened peritreme around spiracles. Spiracular openings large with complex of echinoid-like papillae (Figs. 13, 14). Prothoracic shield, pinacula, and anal plate scarcely differentiated from adjacent cuticle. Thoracic and abdominal segments with scattered, clear warts or excrescences; these more pronounced in size on abdominal segments (Fig. 11);

excrecescences numerous below level of spiracles on both thorax and abdomen. Setae very short, thin and inconspicuous, few longer than height of spiracle, even those of anal plate scarcely longer than height of enlarged A8 spiracle (Figs. 5). Two SV setae on T1, one on T2 and T3, two on A1, three on A2–A6, and one on A7–A9. Head (Figs. 2, 3, 5–9): unpigmented, shallowly creased or roughened anteriorly with low wartling rearward (Fig. 7); setae short and inconspicuous; frons extending about halfway to epicranial notch. Labrum narrow, less than twice as wide as deep, shallowly notched (Figs. 2, 6). Maxillolabial complex as in Figs. 7–9; labial palpus about half length of spinneret; pore apical (Fig. 9). Mandibles as in Fig. 4, with teeth poorly developed; unpigmented except for contrastingly blackened, toothed, distal margin. Thorax (Figs. 5): T1 swollen above, about 15% higher than T2 (receiving head in living larvae) (more pronounced in Fig. 5 than our other pickled individuals); well-developed cervical gland (Figs. 5, 10), evertng in some pickled specimens). SD1 and SD2 subequal on T2 and T3, otherwise SD2 reduced, and closely positioned near spiracle on A1–A8. Abdomen (Figs. 1, 11–14): A8 with exaggerated hump, rising to a middorsal prominence crowned by single excrescence (Fig. 11). L1 closely set to spiracle on A1–A6 and A8, but sifted well downward on A7. SD1 on A9 of same thickness as other setae. Crochets uniorbital (Fig. 12); numbering 21–22, 23–24, 25–26, and 27–29 on A3–A6, respectively.

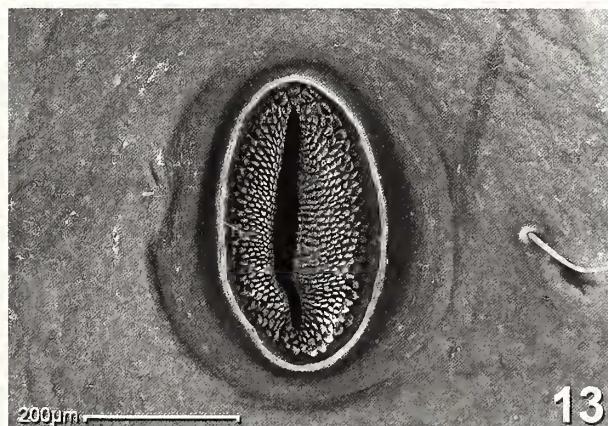
Pupa (Figs. 24–30). Length 13–14 × 5.5–6 mm (n=3). Elongate-oval, widest at A3 (Fig. 24) with distinctive ventral bulge (beyond mid length of wings) (Fig. 25) and dorsal bulge (over A1–A3) (Figs. 25, 28). Integument thick, dark brown with waxy bloom (when dry); surface heavily ornamented with creases and pits: thoracic segments



11



12



13



14

Figs. 11–14. *Miracavira brillians* last instar. (11) A6–A10, lateral. (12) Prolegs on A6. (13) A8 spiracle, head to left. (14) Detail of 13.

deeply coriaceous with parallel creasing along axes of legs and antennae; abdominal segments with numerous, closely set, crater-like depressions; caudal transverse ridges on A4–A6 micropunctate. Setae minute, less than $\frac{1}{2}$ width of spiracle and difficult to locate except about cremaster on A10. Cremaster with horn-like spur directed laterad (Fig. 29). No mouthparts visible; wings ending at caudal reach of A4; legs and antennae as in Figs. 26, 27. Spiracles nearly elliptical; that on A8 rudimentary (Fig. 28).

Life Cycle. Eggs were laid individually with an adhesive (Fig. 15). Those held at ambient temperature at the collection site hatched after seven days ($n > 50$). A portion of the chorion was consumed at eclosion. Larvae passed through five instars. The first three instars each lasted about 3–5 days, the fourth instar 6–8 days, and the final instar 7–14 days (Table 1). Most larvae matured in 4 weeks. Not surprisingly, given this rate of rapid development, larvae often fed both day and night (and remained at rest adjacent to feeding site). Prepupae tunneled into leaf litter or below ground, where they fashioned a loose cocoon of off-white silk. Pupation occurs 3–4 days after the cocoon is completed. Duration of the pupal stage is expected to be close to 10.5 months for those individuals hatching after a single year, although other psaphidines are known to overwinter multiple times and up to 7 years (Wagner et al. 2009, Dale Schweitzer unpublished data).

Life History Notes. *Miracavira brillians* is a specialist on *Ptelea trifoliata* (and perhaps other *Ptelea* in Mexico) (Family Rutaceae). While new foliage is preferred, especially by early instars, mature leaves, including those that are somewhat blighted, are ingested and satisfactory for development. Such is not the case for many eastern psaphidines which will struggle and starve if not offered young, not-yet-hardened foliage (Wagner 2005, Wagner et al. 2009).

The first through at least the third instars spin a thin sheeting of silk along a leaf edge and then feed on

adjacent tissues, keeping the prolegs engaged in silk. Disturbed first instars may balloon downward on a line of silk. The first two instars skeletonize the upper side of the blade over and adjacent to a leaf edge, although towards the end of the second instar some larvae chew through the blade. Third instars largely confine their feeding to a leaf edge, either eating small holes through the blade or carving out cavities from a leaf edge. Some fourth instars also spin a silken sheet over the lamina into which the crochets are engaged, especially prior to

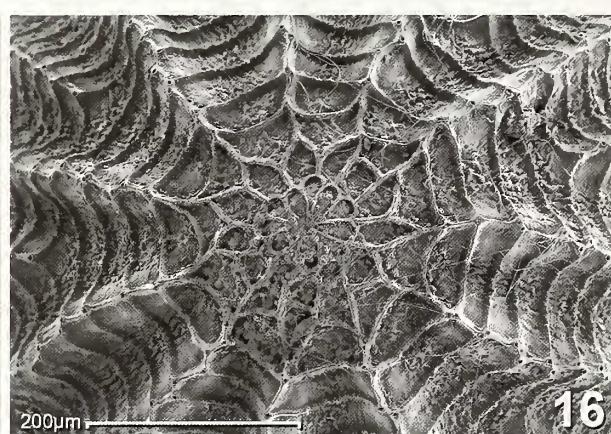
TABLE 1. Head capsule widths and development times for *Miracavira brillians*.

Stage/ Instar	Head capsule widths in mm: range, mean, # obs.	Approx. length in days; stragglers excluded ¹
Egg		Aug 16 – Aug. 23
1st	0.45–0.48, 0.47, 11	Aug. 23 – Aug. 26
2nd	0.73–0.79, 0.77, 15	Aug. 26 – Aug. 31
3rd	1.14–1.18, 1.12, 9	Aug. 29 – Sept. 5
4th	1.82–1.98, 1.8, 18	Sept. 1 – Sept. 10
5th	2.88–2.90, 2.89, 2	Sept. 7 – Sept. 30
Pupa	8	Sept 15 –

¹ Data combined from single clutch reared as two cohorts: one indoors in Hereford Arizona at ambient temperature and a second cohort reared at 23° C in a lab at the University of Connecticut. A third cohort of larvae from the same female sleeved (outdoors) in Hereford had accelerated development with larvae maturing after only 3–3.5 weeks.



FIGS. 15–16. *Miracavira brillians* egg. (15) Chorion sculpturing, note adhesive. (16) Micropylar area.





FIGS. 17–23. *Miracavira brillians* (17–22) and *Amphipyra pyramidoides* (23) larvae. (17) First instar. (18) Second instar. (19) Third instar. (20) Fourth instar. (21) Fifth instar. (22) Fifth instar, head. (23) Fifth instar *Amphipyra pyramidoides*.

a molt. Last instars typically rest off the blade, firmly grasping petioles or shoot tips.

Larvae of all instars are difficult to remove from their perch, either because they securely engage the prolegs into their silken sheet (first four instars) or because they hold onto the petiole or rachis tenaciously (last instar). Early instar caterpillars spin silk in advance of any change in position. Most remarkably, two of three preserved (boiled) last instars retained their grip on leaf tissue throughout a five-minute boiling period and to this writing remain firmly attached (in 70% alcohol) to the petiole to which they had initially secured themselves. It is remarkable that the larvae would hold on with such leviathan force, and one must wonder if this behavior has evolved, at least in part, to help the

larvae maintain their purchase in the violent squalls of the American Southwest's monsoon season. Silk also aids molting as larvae secure the anal prolegs into the sheeting prior to molting. Almost without exception, cast skins are consumed following the molts.

First through third instars, when disturbed, sometimes vibrate rapidly from side to side. This behavior was most often noted in first instars and could sometimes be induced with a wisp of air. Vibrating was not observed in fourth and fifth instars.

As in other trifid noctuids, the early instars scarcely use the first two pairs of abdominal prolegs when crawling. The anterior pair (on A3) is only about half the size of those on A5 and A6. Prolegs on A4 are also reduced in size. Even while perched, first, and to some

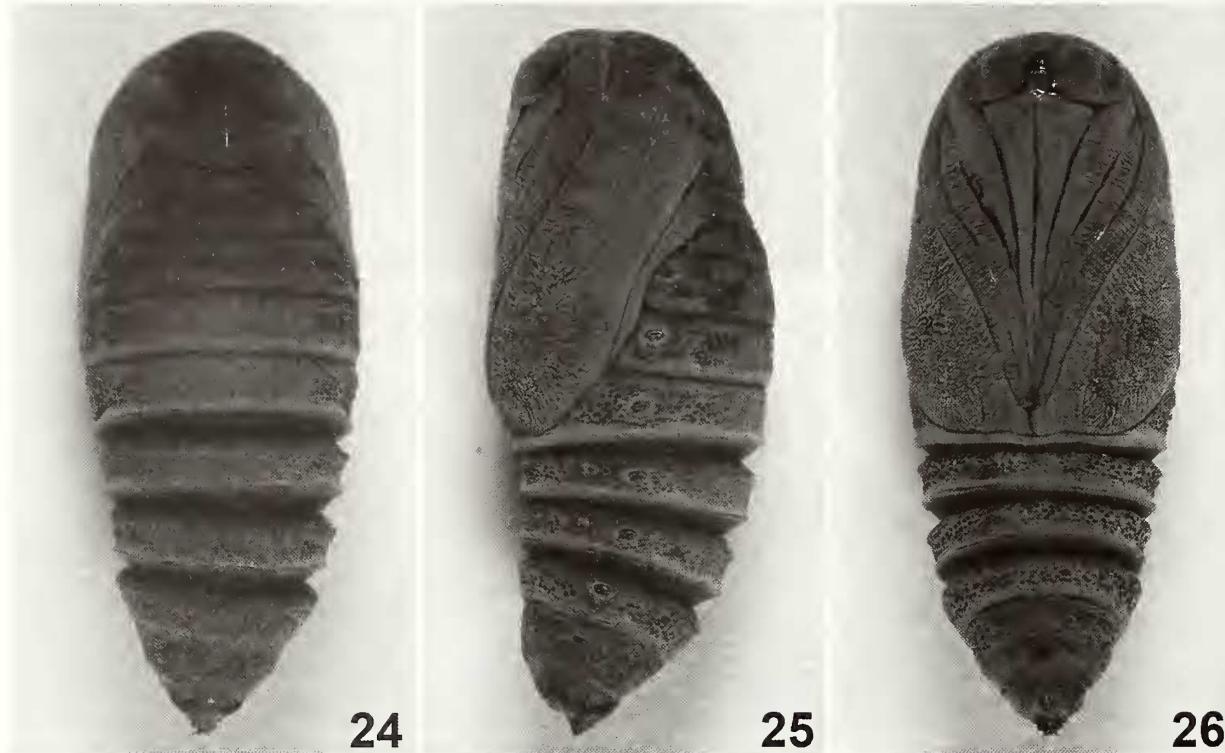
extent second instars, elevated the anterior end of the body such that the first two pairs of prolegs were either not in contact with the leaf/silk or only weakly secured.

Miracavira is exceedingly sedentary, often occupying the same perch for three instars. The caterpillar's site fidelity contrasts markedly with *Amphipyra pyramidoides* Guenée, a familiar eastern species that *Miracavira* somewhat resembles. *A. pyramidoides* was cited by Heinrich (1979) as a species that plays "the shell game" with its (avian) predators by frequently changing its location, especially after feeding, and in so doing, removing itself from leaves that it has damaged and which might reveal its whereabouts to natural enemies.

The first two instars perch extended along a leaf margin where their coloration is stunningly cryptic (we found it difficult to accurately count larvae without the aid of reading glasses or a lens). Fourth and fifth instars perch with the head, partially drawn into the prothorax, craned back over and held above or pressed against the abdomen; the forelegs are commonly folded across the mouthparts. In middle instars the head is held over the dorsum of the middle abdominal segments. In the last instar the head is pushed even farther rearward, and in the extreme, the frons is held against the anterior face of

the abdominal hump (segments 7 and 8) (Fig. 21) or drawn to one side. Again, the first two pairs of legs are held forward and flat against the body; the metathoracic legs are held outward. The anal prolegs are mostly covered by the anal plate. This resting (not alarm) posture presumably provides a case of protection through non-resemblance—the larva is most uncaterpillar-like in appearance. In the fourth and especially fifth instars, the larva becomes increasingly blue-green and a whitish bloom develops over the dorsum, enhancing the insect's countershading (Cott 1940, Edmunds 1974, Ruxton et al. 2004) (the caterpillar's pale dorsum is directed downward when the insect is perched on a petiole or twig). Whether *Miracavira*, in fact, enjoys the evolutionary benefits of non-resemblance and/or countershading will require testing, but there can be little argument that the insect's posture protects the head from direct strikes: at rest the head is pulled beneath the horn-like rim of the prothorax and the front is held proximate to the abdominal hump.

TAXONOMIC PLACEMENT. In 2005 Fibiger and Lafontaine transferred *Miracavira* into the Acronictinae on the basis of the heavily sclerotized, apically positioned clasper, and pattern similarities with the Old



FIGS. 24–26. Pupa of *Miracavira brillians*. (24) dorsal. (25) lateral. (26) ventral.

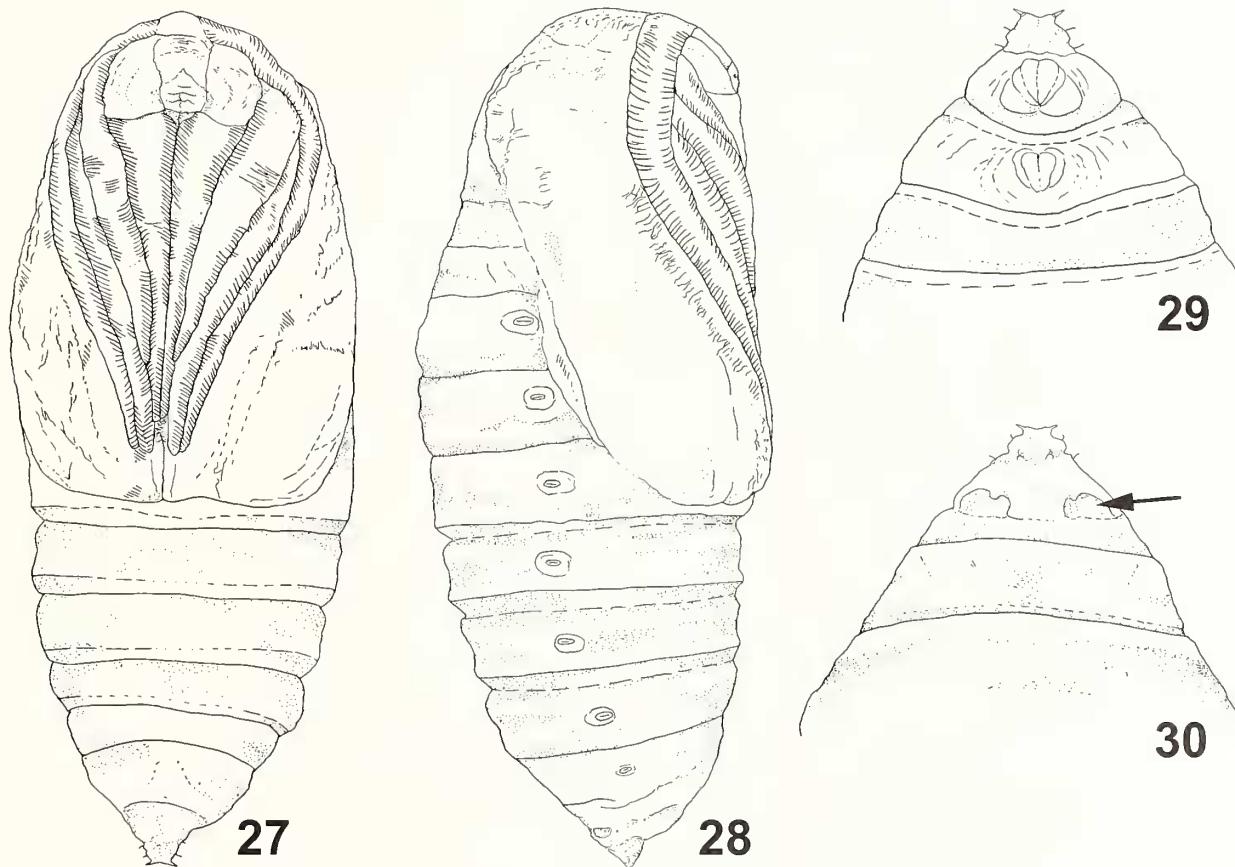
World acronictine genera *Nacna* Fletcher and *Diphtherocome* Warren. Neither author had early stages of the insect for examination. The larva of *M. brillians* lacks acronictine features as defined by Crumb (1956), Kitching and Rawlins (1998), and Wagner (2007a, 2007b); i.e., *Miracavira* bears only primary setae, verrucae are absent, there is only one seta on the L3 pinaculum on A1–A8, and the dorsal pinacula are distant on both the meso- and metathorax.

The caterpillar of *Miracavira* shares a number of features common to the Psaphidinae (and Amphipyrinae): A8 is humped, the spiracular stripe continues around the anal plate, the dorsal pinacula are whitened, and the head is partially retracted into the thorax (Wagner et al. 2009). The pupa of *Miracavira* possesses dorsal pits on A10 (Fig. 30), a feature regarded to be synapomorphic for the subfamily Psaphidinae by Kitching and Rawlins (1998). Below we expand on our argument that *Miracavira* is a

Amphipyrinae: Psaphidini, and best fits within the subtribe Feraliina.

Poole (1995) tentatively associated the Psaphidini and Feraliini on the basis of four characters: the thick, hairy vestiture of the adults; spring flight of the adults; irregular spinning of the tarsi; and enlarged bulla posterior to the tympanal hood. The first of these are common among spring-flying noctuids; the fourth character also was noted by Poole (1995: 162) to occur in other subfamilies. Kitching and Rawlins (1998) identified the shared dorsal pits A10 of the pupa as an additional feature strengthening the association between the two tribes. Many of the genera that we examined over the course of this study were found to possess a dorsally lengthened, almost hood-like tegumen. Beyond these few characters, the Psaphidini and Feraliini are rather structurally divergent.

Psaphidini have a “claw” at the apex of the foretibia (actually a spine-like seta), a character common



Figs. 27–30. Line drawings of female pupa. (27) ventral. (28) lateral. (29) A8–A10, ventral. (30) A8–A10, dorsal; arrow points to A10 pits.

throughout the Oncocnemidinae, Psaphidinae, and Stiriinae, but frequently lost secondarily (the tibial "claw" in the Cuculliinae is a spine not a seta). The male abdomen has the seventh tergite greatly enlarged and heavily sclerotized, a peculiar character shared with two other psaphidine tribes, Nocloini Poole and Triocnemidini Poole (but absent in the Feraliini). In the male genitalia (e.g., Fig. 31), the uncus is simple, tapered at the apex into a spine; the coronal setae at the valve apex are weak; the clasper is a slightly more heavily sclerotized area on the ventral margin of the valve with an elongated, lightly sclerotized, setose ampulla; the vesica is a simple expanded tube covered with spike-like cornuti with a single larger cornutus at the apex in most species. We consider most of these features to be plesiomorphic within the Psaphidinae because they are also present in the Oncocnemidinae and Stiriinae.

Typical Feraliini (only the genus *Feralia*, Figs. 32, 33) depart from the Psaphidini in several ways: the apical spine on the tibia is lost; the uncus is divided apically into a pincer-like structure; the apical corona on the valve is weak or absent; the clasper and ampulla are absent; a heavily sclerotized, tapered digitus is fused to the inner surface of the valve and narrows into a subapical pollex-like process; the vesica typically is rounded with two diverticula (e.g., Fig. 33b), each covered with long spike-like cornuti. In some species one or both of these diverticula are reduced (e.g., Fig. 32b).

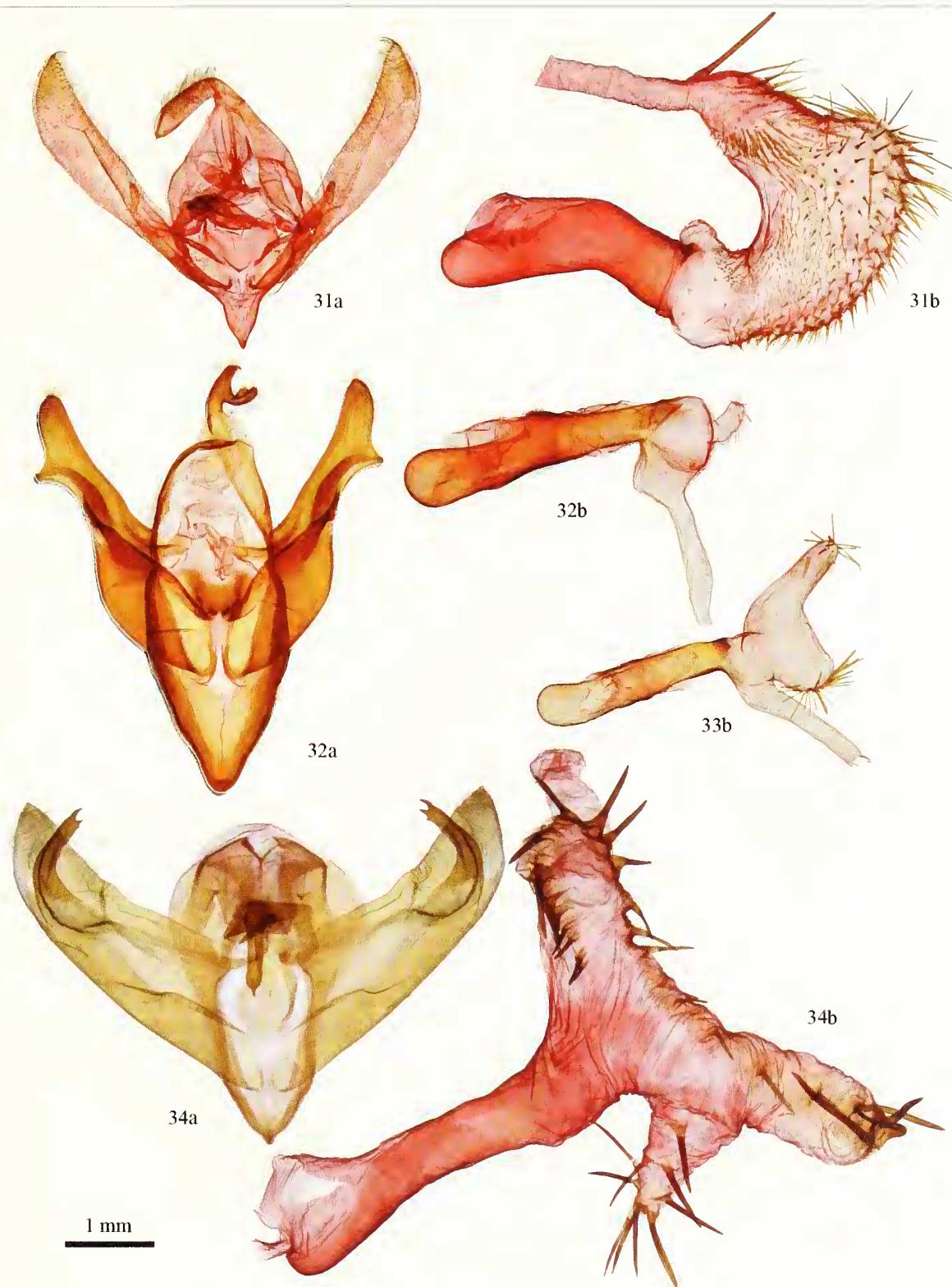
Both larval and adult characters indicate that *Miracavira* has a close phylogenetic affinity to the Feraliini Poole. The emerald green and, more importantly, transparent, second and third instars of *Miracavira* resemble those of *Feralia*. Like *Miracavira*, larvae of *Feralia* are exceedingly sedentary in habit (McFarland 1963), and at least in later instars, caterpillars of both genera accept older foliage, a trait not shared with spring-active genera of Psaphidini. Adult coloration of *Miracavira* and *Feralia* are similar—both *M. brillians* and *M. sylvia* (Dyar) were originally described as members of the genus *Feralia* (or its synonym *Momaphana*); evidently, the principal reason that the two species were removed by Franclemont (1937) was because the adults lacked eye lashes. Adults lack the apical digging claw on the foretibia common to Psaphidini.

Miracavira has highly divergent male genitalia (Fig. 34, note we figure *M. sylvia*, the type species of the genus), but within the psaphidine is structurally more similar to genera in the Feraliini than to those in the Psaphidini. *Miracavira* and other genera have diverticula in the vesica covered with spike-like cornuti

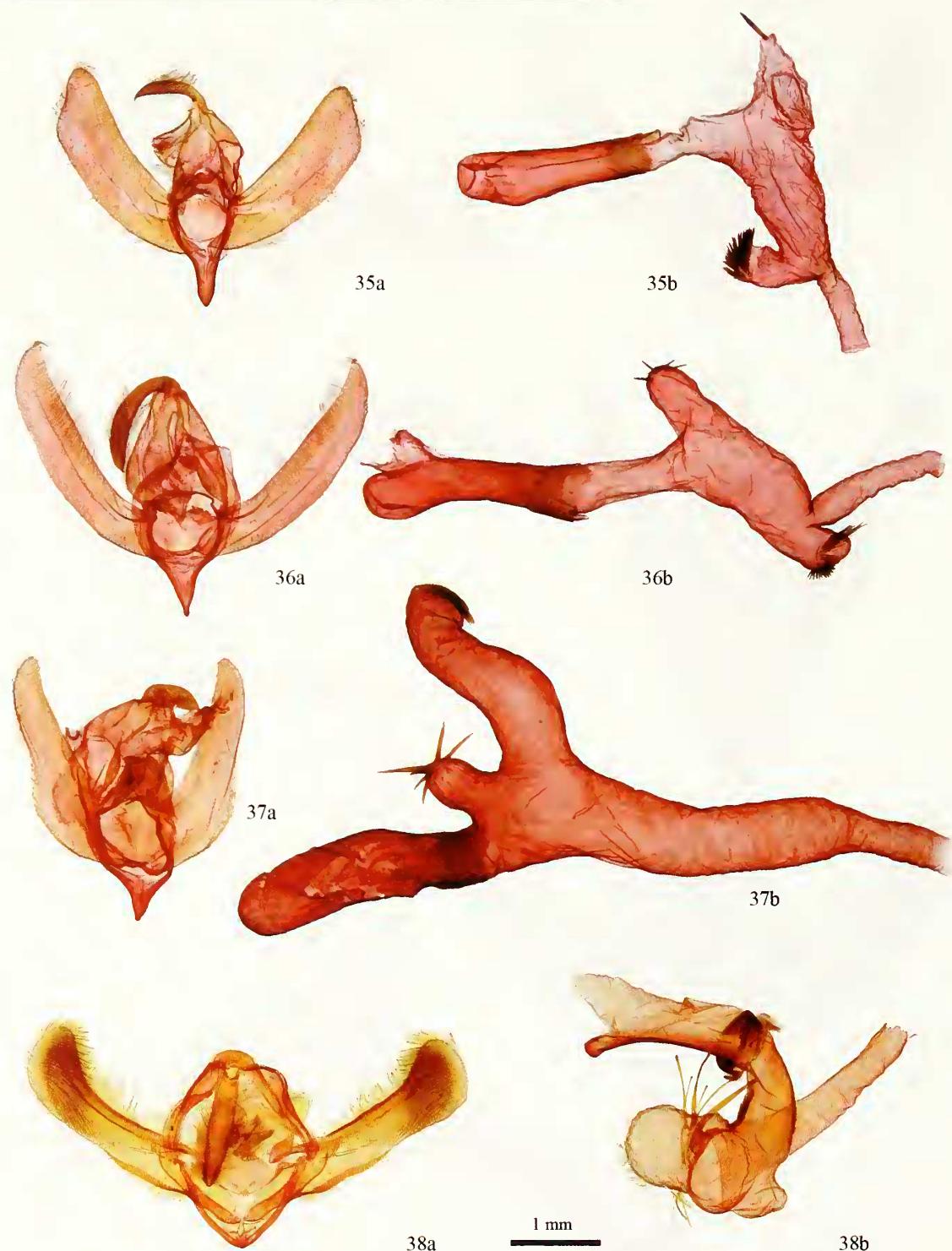
(in *Miracavira* the vesica has three large diverticula, each covered with long spike-like cornuti). In both *Feralia* and *Miracavira* the ampulla of the clasper and the corona are lost. Differences in genitalia between the two genera are extreme and seem to overshadow the similarities: *Miracavira* has no trace of a digitus, the uncus is typical of other psaphidines, not highly modified as in *Feralia*, the dorsal part of the tegument is highly modified, and the clasper is massive (lost in *Feralia*).

We associate three other genera (*Paratrachea* Hampson, Fig. 35; *Apsaphida* Franclemont, Fig. 36; and *Viridemas* Smith, Fig. 37) with the Feraliini on the basis of the loss of the tibial "claw," the loss of the clasper and ampulla on the valve, the dorsally expanded tegumen, and the presence of two cornuti-covered diverticula in the vesica. These three genera can be associated with each other by a brush-like structure formed by a tight clustering and reduction in length of the cornuti at the apex of the diverticulum closest to the ductus ejaculatorius. Two of these genera, *Paratrachea*, based on *P. viridescens* (B. & McD.), and *Apsaphida*, can be associated as sister taxa by the close similarity of the shape of the vesica.

Connections to the Amphipyrinae. Intriguing are the similarities between the larvae of *Miracavira brillians* and *Amphipyra pyramidoides* (Amphipyrinae) (Figs. 21, 23). Shared features include the raised and rather angulate eighth abdominal segment; a yellow middorsal wart on A8; a similar set of middorsal, subdorsal, and spiracular stripes, with the latter weakening over the anterior abdominal segments; and bulging yellow excrescences (Fig. 11) over the upper half of the body and smaller wartling below the level of the spiracles. *Miracavira* caterpillars and those of some *Amphipyra* (including the Palearctic species *A. pyramidaea* L. and *A. berbera* Rungs) often have a decided blue-green aspect to the ground color—an unusual coloration among caterpillars. In both genera the head is partially retracted into the thorax (as is the case with many psaphidines). An especially striking similarity is the spiracular coloration: both *Miracavira brillians* and *Amphipyra pyramidoides* have a broad black ring (?peritreme) about the spiracle that, in turn, is surrounded by a pale halo (Figs. 21, 23). Late instars of the two genera rest with the anterior end of the body lifted and well removed from the perch (Figs. 21, 23). Members of both *Amphipyra* and *Feralia* also bridge the phenotypic gap between the Amphipyrinae and Psaphidinae. The larval coloration and patterning of *Amphipyra tragopoginis* (Clerck), and in particular its striping and humped eighth abdominal segment are reminiscent of North American *Feralia* species. *Feralia*



Figs. 31-34. Male genitalia: (a) genital capsule; (b); aedeagus with vesica everted. (31a, b) *Psaphida resuncus* Walker. (32a, b) *Feralia jocosa* (Guenée). (33b) *Feralia sauberi* (Graeser). (34a, b) *Miracavira sylvia* (Dyar).



Figs. 35-38. Male genitalia: (a) genital capsule; (b) aedeagus with vesica everted. (35 a, b) *Paratrachea viridescens* (Barnes & McDunnough). (36 a, b) *Apsaphida eremna* Franclemont. (37 a, b) *Viridemas galena* Smith. (38 a, b) *Amphipyra tragopoginis* (Clerck).

febrialis Grote, a western oak-feeding member of the genus, has an exaggerated, sharply angulate, hump on A8, comparable to that of *Miracavira brillians* and *Amphipyra pyramidoides*.

The male genitalia of the Amphipyrinae and Psaphidinae also share many characters. In the Amphipyrinae the clasper and ampulla may be lightly sclerotized with the ampulla finger-like and setose (e.g., *Amphipyra tragopoginis*, Fig. 38); or similar to those of the Psaphidinae with the ampulla large, spike-like, and heavily sclerotized (e.g., *Pyrois effusa* (Boisduval)); or lost (e.g., *Amphipyra pyramidoides* and many *Feraliini*). Also, in both the Amphipyrinae and Psaphidinae the vesica is covered with long, spike-like cornuti arising from stout bases. Two derived amphipyrine character states (not shared by Psaphidinae) are the large, broad, flat pleural sclerite and the disproportionately massive uncus.

In sum the similarities between the Amphipyrinae and Psaphidinae show that the Psaphidinae would be best subsumed within the Amphipyrinae as the tribe Psaphidini, and the *Feraliine* as a subtribe of the latter. Evolutionary relationships among the currently recognized amphipyrine-psaphidine tribes, and in particular the Nocloini and Triocnemidini, need study. Towards this end, we encourage others to secure and preserve early stages of the Nocloini and Triocnemidini (which are all but unknown) and preserve tissue for molecular studies.

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